

Improving Estimation of Wolf Recruitment and Abundance, and Development of an Adaptive Harvest Management Program for Wolves in Montana



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INTRODUCTION

Wolves (*Canis lupus*) were reintroduced in the northern Rocky Mountains (NRM) in 1995, and after rapid population growth were delisted from the endangered species list in 2011. Since that time, states in the NRM have agreed to maintain populations and breeding pairs (a male and female wolf with 2 surviving pups by December 31; USFWS 1994) above established minimums (≥ 150 wolves and ≥ 15 breeding pairs within each state). Montana estimates population size every year using patch occupancy models (POM; MacKenzie et al. 2002, Rich et al. 2013, Miller et al. 2013, Bradley et al. 2015), however, these estimates are sensitive to pack size and territory size, and were developed pre-harvest. Reliability of future estimates based on POM will be contingent on accurate information on territory size, overlap, and pack size, which are expected to be strongly affected by harvest. Additionally, breeding pairs, which has proven to be an ineffective measure of recruitment, are determined via direct counts. Federal funding for wolf monitoring has ended in states where wolves are delisted, and future monitoring will not be able to rely on intensive counts of the wolf population. Furthermore, monitoring has become cumbersome and less effective since the population has grown. With the implementation of harvest, it is pertinent to predict the effects of harvest on the wolf population and continue to monitor to determine effectiveness of management actions to make informed decisions regarding hunting and trapping seasons.

STUDY OBJECTIVES

Our 4 study objectives are to:

1. Improve estimation of recruitment.
2. Improve and maintain calibration of wolf abundance estimates generated through POM.
3. Develop a framework for dynamic, adaptive harvest management based on achievement of objectives 1 & 2.
4. Design a targeted monitoring program to provide information needed for robust estimates and reduce uncertainty in the AHM paradigm over time.

Two PhD students are addressing the 4 study objectives as part of Project 1 (Sarah Sells) and Project 2 (Allison Keever; Fig. 1).

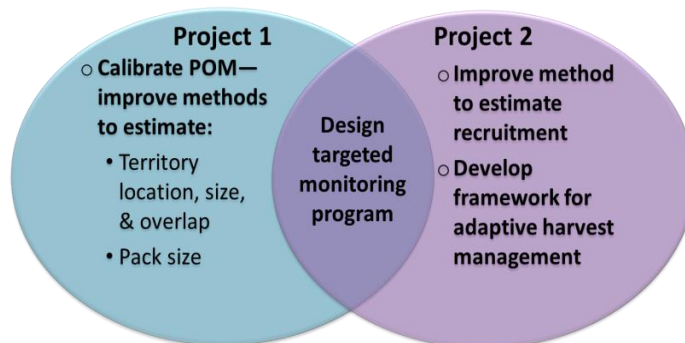


Fig. 1. Objectives for this project are being addressed under 2 separate projects.

DELIVERABLES

1. A method to estimate recruitment for Montana's wolf population that is more cost effective and biologically sound than the breeding pair metric.
2. Models to estimate territory size and pack size that can keep POM estimates calibrated to changing environmental and management conditions for wolves in Montana.
3. An adaptive harvest management model that allows the formal assessment of various harvest regimes and reduces uncertainty over time to facilitate adaptive management of wolves.
4. A recommended monitoring program for wolves to maintain calibration of POM estimates, determine effectiveness of management actions, and facilitate learning in an adaptive framework.

LOCATION

This study encompasses wolf distribution in Montana and Idaho (Fig. 2). Additional data will come from Yellowstone National Park for the territory models developed under objective 2.

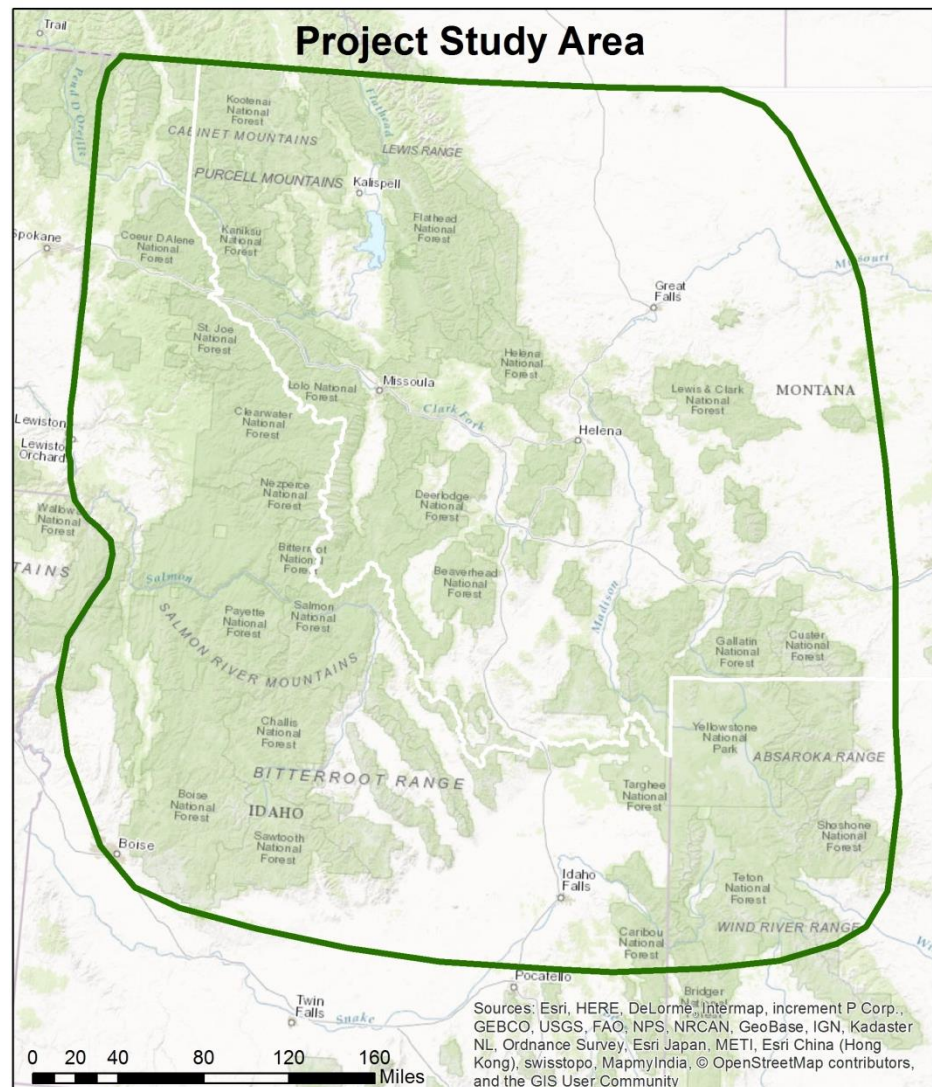


Fig. 2. The project study area includes wolf distribution in Montana and Idaho, as well as Yellowstone.

GENERAL PROGRESS

The 2 PhD students started their programs in January 2015 (Fig. 3).

Much of year 1 was devoted to literature reviews on animal behavior, carnivores, modeling, optimal foraging, etc. and determining approaches

for the dissertations. The students also formed and held multiple meetings with their committees, worked on completing coursework requirements, and finalized research statements. Additional efforts focused on communicating with wolf specialists, identifying target packs for collaring, managing collar orders and data, and helping coordinate contracts and capture plans for winter aerial captures for January and February 2016. The students also met with wolf specialists in the field to learn more about the wolves in each region, and coordinated and held meetings with the specialists to plan future project efforts.

Most activities from year 1 continued through year 2, including conducting literature searches, taking classes, holding committee meetings, communicating with wolf specialists, managing collar orders, managing data, etc. The students joined MFWP wolf specialists to assist with a month of trapping.

The students also focused on meeting University requirements and deadlines. The students each successfully completed and defended dissertation proposals. The students have also completed comprehensive exams (S. Sells) or are taking them in spring 2017 (A. Kever).

Project deliverables in years 2017–2020 will include an empirical recruitment model; theoretical territory, group size, and recruitment models; draft and final AHM models; and final territory and pack size models. The students have been working on the empirical recruitment model and the theoretical territory model deliverables towards meeting objectives 1 and 2. Updates are provided below on these objectives. (Additional details on objectives 3 and 4 are available in the 2016 report.)

DATA COLLECTION SUMMARY

Trapping efforts have continued since 2014:

- There have been 51 successful captures directly related to this project through 2016.

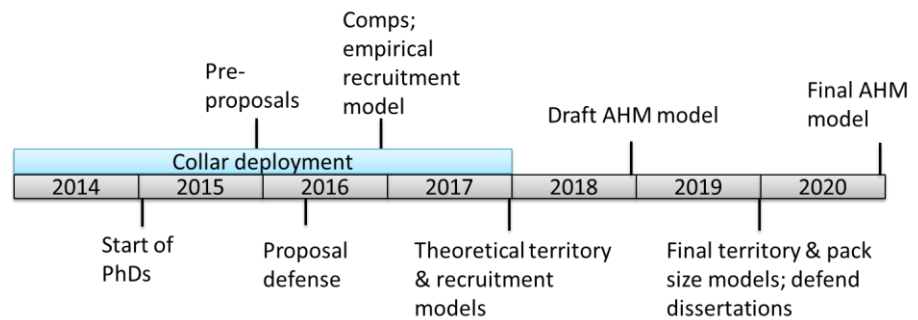


Fig. 3. Project timeline.

- Collars were deployed in approximately 41 packs (this number is fluid as wolves disperse).
- Using ground and aerial captures:
 - 10 collars were deployed in 2014.
 - 14 collars were deployed in 2015.
 - 27 collars were deployed in 2016.
- These collars have yielded >20,000 locations of wolves (Fig. 4).
- Despite collar removals, harvests, other mortalities, and some collar losses, 24 collars remained deployed at the end of 2016.

Collaring efforts will continue via ground and aerial captures through 2017.

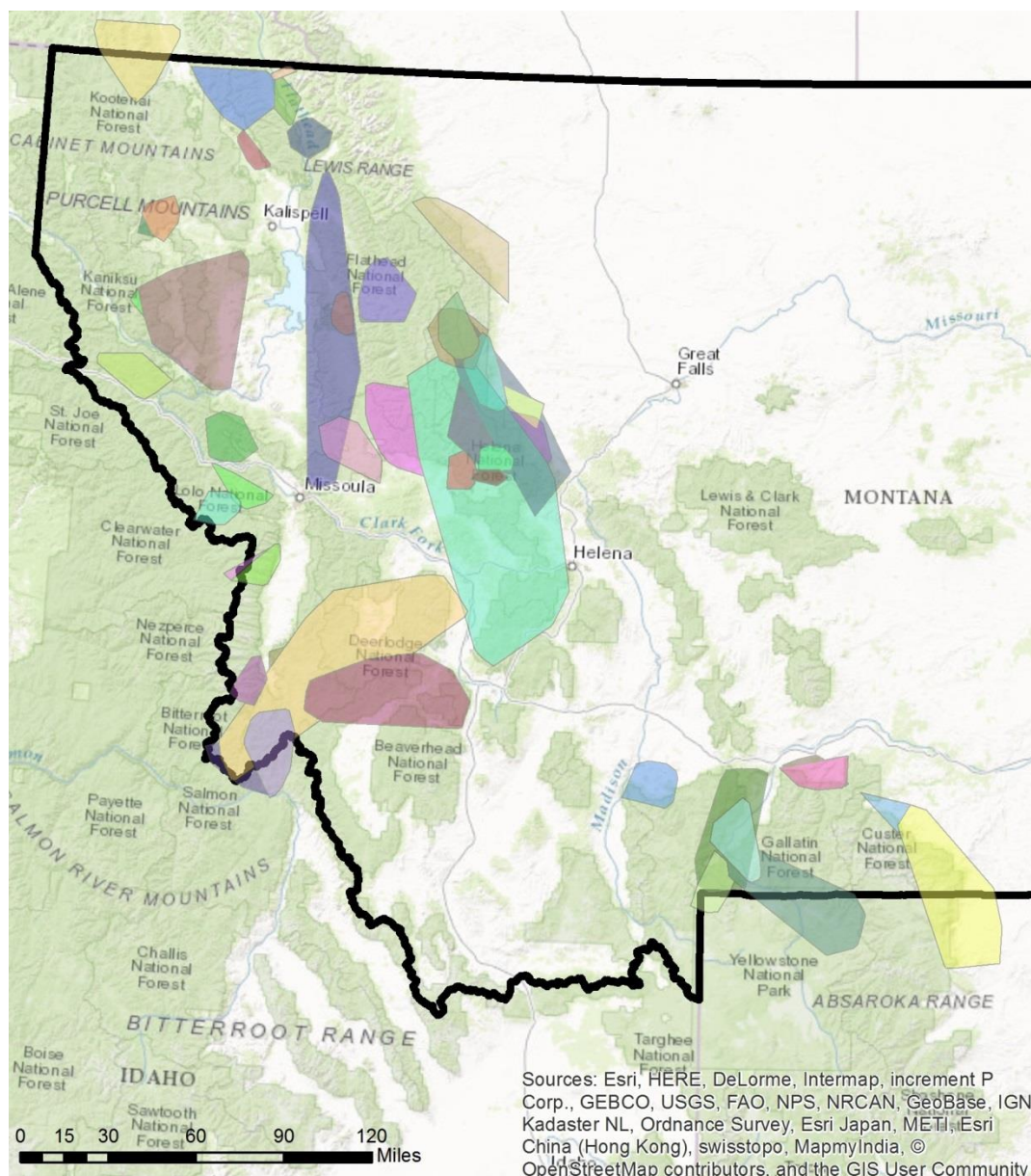


Fig. 4. Locations of wolves collared for this project, 2014–2016. Colors represent different wolves. Note that some polygons include dispersal from original pack's territory.

PROGRESS ON OBJECTIVES

Objective 1: *Improve estimation of recruitment.*

1.1 Background

Estimating recruitment (i.e., number of young produced that survive to an age at which they contribute to the population) of wolves can be difficult due to their complex social structure. Wolves are cooperative breeders, and pack dynamics (e.g., pack tenure, breeder turnover, and number of non-breeding helpers) can affect recruitment and pup survival (e.g., Ausband et al. 2015). Cooperative breeding often relies on the presence of non-breeding individuals that help raise offspring (Solomon and French 1997), and reduction in group size can lead to decreased recruitment in cooperative breeders (Sparkman et al. 2011, Stahler et al. 2013). Human-caused mortality through both direct and indirect means (Ausband et al. 2015) and prey biomass per wolf (Boertje and Stephenson 1992) have been shown to affect recruitment. As a result, it will be important to consider the effects of harvest, pack dynamics, wolf density, and prey availability on recruitment.

Further challenges of estimating recruitment include the size of the wolf population and limited time and funding for monitoring. Currently, MFWP documents recruitment through visual counts of breeding pairs (a male and female wolf with 2 surviving pups by December 31; U.S. Fish and Wildlife Service 1994). These counts, however, are likely incomplete due to the large number of wolves in the population. Federal funding for wolf monitoring in Montana and Idaho is no longer available. States therefore fund their own monitoring programs, and future monitoring will not be able to rely on intensive counts. A breeding pair estimator (Mitchell et al. 2008) could be used to estimate breeding pairs, but this requires knowing pack size; such data are hard to collect given the size of the wolf population. Additionally, the breeding pair metric is an ineffective measure of recruitment because it provides little insight into population growth rate or the level of harvest that could be sustained. Recruitment could be estimated by comparing visual counts at the den site to winter counts via aerial telemetry (Mech et al. 1998) or by marking pups at den sites (Mills et al. 2008). An alternative method could include non-invasive genetic sampling (Ausband et al. 2015) at predicted rendezvous sites (Ausband et al. 2010). These methods, however, may not be feasible on large scales due to budget and staff constraints. Existing monitoring efforts yield insufficient data to estimate recruitment using traditional methods; therefore a new approach is needed that does not rely on extensive data.

1.2 Goals and General Approach

Our objective is to develop an approach to estimate recruitment that is more tractable, cost effective, and biologically credible than the breeding pair metric. Integrated population models can be a useful tool for demographic analyses from limited data sets, and can increase precision in estimates (Besbeas et al. 2002). We will develop a per capita integrated population model

(hereafter IPM) to estimate recruitment and evaluate the relationship between recruitment and factors that may cause spatial and temporal variation in wolf recruitment using collar, count and hunter survey data from 2007–2016 in Montana. A generalized linear model can then be used to evaluate variation in recruitment across time and space.

The resulting statistical model will relate covariates and recruitment. It will not, however, improve understanding of the mechanisms that cause recruitment to change. Recruitment depends on a pack's success in breeding and giving birth, as well as litter size and pup survival. Whether a pack successfully breeds and gives birth or not is primarily determined by the survival of the breeding pair in the pack. Conversely, pup survival may be affected by helper presence, prey availability, disease outbreaks, and human-caused mortality (Goyal et al. 1986, Boertje and Stephenson 1992, Johnson et al. 1994, Mech and Goyal 1995, Fuller et al. 2003, Ausband et al. 2015). Unfortunately, there are few data to estimate the contribution of those factors to overall pup recruitment, so we will also develop a mechanistic model of recruitment to theoretically explore the effects of human-caused mortality, prey availability, multiple litters per pack, disease outbreaks, and group size on the different components of recruitment. The probability a pack successfully breeds and reproduces, litter size per pack, and pup survival all determine pup recruitment. Hypotheses about how factors such as disease, harvest, or prey availability affect these parameters can be explored using linear or non-linear models and then multiplied together. Different models can be developed that represent different hypotheses. Those different hypotheses will result in different predictions of recruitment if those hypotheses were correct. The model predictions can be compared to estimated recruitment from the IPM to determine which hypotheses have most support.

1.3 Progress

Overview:

We are currently developing the IPM model to estimate recruitment in program R (R Core Team 2014) in a Bayesian framework using package R2jags (Su and Yajima 2015) to communicate with JAGS (Plummer 2003). The model includes a series of sub-models, including a 1) population, 2) group count, 3) survival, and 4) occupancy model (Fig. 5). We are currently simulating data to test the accuracy of the IPM. Once we simulate data we will evaluate how many data (collar and group count data) are needed to maintain reliable estimates of recruitment. Then, we will use hunter survey, group count, and collar data to estimate recruitment across the state of Montana. So far, we have the population and group count models and are fixing occupancy and survival to test a simpler version of the model. The population and group count models are specified as follows:

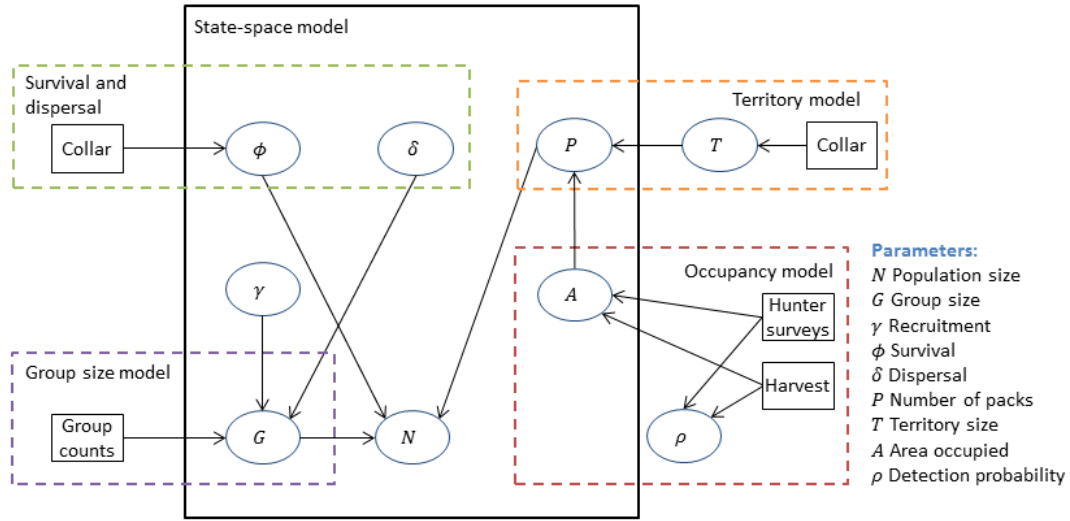


Fig. 5. Directed acyclic graph of a per capita integrated population model for wolves. The boxes represent data sources and the circles represent parameters.

a) Population level model.

We first linked changes in population size to demographic rates. Population size is estimated using the number of packs (P) estimated from POM and mean group size (\bar{G}) which is estimated from group counts. The population level model is then

$$P_{k+1,r} \bar{G}_{k+1,r} = P_{kr} \bar{G}_{kr} \phi_{kr} (1 + \omega - \varepsilon) + P_{kr} \bar{\gamma}_{kr}$$

where ϕ_{kr} is survival probability that is estimated using collar data, ω is immigration rate into the population as establishment of new packs (i.e., colonization rate), ε is emigration rate as packs leaving the population (i.e., extinction rate), and $\bar{\gamma}_{kr}$ is mean recruitment per pack for year k in region r .

b) Group count model.

We used group count data to estimate mean group size (\bar{G}) and mean recruitment per pack ($\bar{\gamma}$). Here, we assume recruitment to be the number of pups produced and that survive 1 year. The group model is

$$G_{k+1,ri} = G_{kri} \phi_{kri} (1 + \alpha - \delta) + \gamma_{kri} + \sigma_{kr}$$

where α is immigration rate into a pack, δ is emigration rate from a pack, γ_{kri} is number of pups recruited per pack, and σ_{kr} is process error by year and region.

Preliminary results:

With simulated data we know “truth,” and can compare our estimates to truth. When we ran the simple model with occupancy and survival fixed, we found that our estimates of mean group size were very accurate (Fig. 6), and our estimates for total population size and recruitment were also accurate using only group count data from 50 packs.

Summary and Next Steps:

In the future we will add the occupancy and survival models and the collar and hunter survey data. We will evaluate the accuracy and precision of these models using different amounts of data (e.g., number of groups with counts or number of collars) to determine the level of precision that corresponds with different amounts of data.

After we explore the model, we will use data from Montana to estimate recruitment across the state and evaluate the factors that cause spatial and temporal variation in recruitment. Then, we will test the model using field-based recruitment data collected in Idaho.

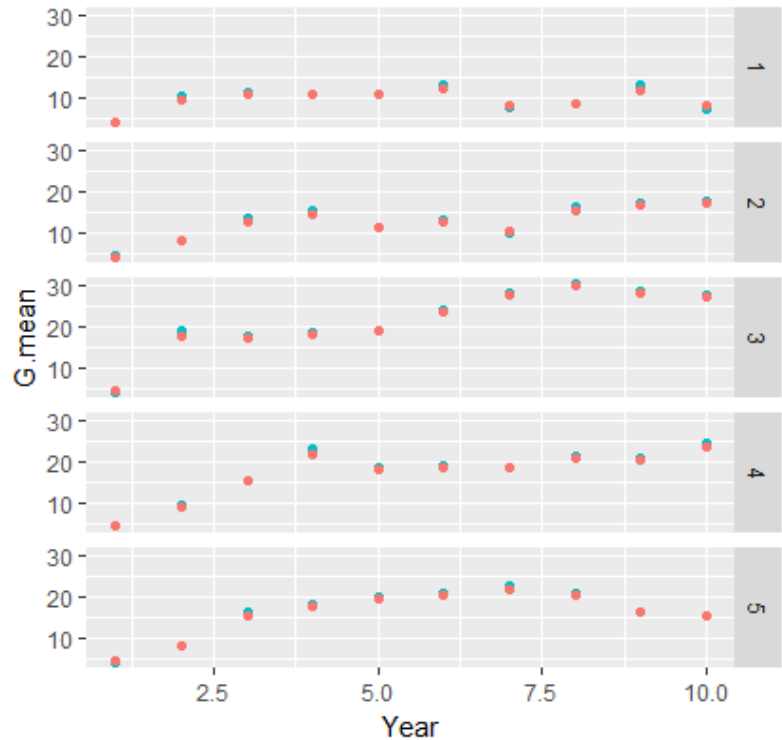


Fig. 6. Estimates (red circles) and truth (blue circles) of mean group size for wolves in Montana in 5 different regions across 10 years. In this analysis, truth was simulated.

Objective 2: *Improve and maintain calibration of wolf abundance estimates generated through POM.*

2.1 Background

Monitoring is a critical, yet challenging, management tool for gray wolves. Since delisting of wolves in 2011, monitoring results help MFWP set management objectives and communicate with stakeholders and the public. Monitoring any large carnivore is challenging, however, due to their elusive nature and naturally low densities (Boitani et al. 2012). This is particularly true for wolves due to increasing populations, decreasing funding for monitoring, and changing behavioral dynamics with harvest.

Abundance estimates are a key component of monitoring (Bradley et al. 2015). Abundance is currently estimated in Montana with 3 parameters: area occupied, average territory size, and annual average pack size (Fig. 7, Bradley et al. 2015). Area occupied is estimated with a Patch Occupancy Model (POM) based on hunter observations and field surveys (Miller et al. 2013, Bradley et al. 2015). Average territory size is assumed to be 600 km² with minimal overlap,

based on past work (Rich et al. 2012). Annual average pack size is estimated from monitoring results. Total abundance (N) is then calculated as: $N = (\text{area occupied} / \bar{x} \text{ territory size}) \times \bar{x} \text{ pack}$.

Whereas estimates of area occupied from POM are expected to be reliable (Miller et al. 2013, Bradley et al. 2015), reliability of abundance estimates hinge on key assumptions about territory size, territory overlap, and pack size (Bradley et al. 2015). Assumptions of fixed territory size and minimal overlap are simplistic; in reality, territories vary spatiotemporally (Uboni et al. 2015). This variability is likely even greater under harvest (Brainerd et al. 2008). Meanwhile, pack size estimates assume all packs are located and accurately counted each year, which is no longer possible due to the number of packs and declining funding for monitoring (Bradley et al. 2015). Since implementation of harvest in 2009, several factors have further compounded these challenges and decreased accuracy of pack size estimates. First, whereas larger packs are generally easier to find and monitor, average pack size has decreased since harvest began (Bradley et al. 2015). Difficult-to-detect smaller packs may be more likely to be missed altogether, biasing estimates of average pack size high. Conversely, incomplete pack counts, especially for larger packs, could bias estimates of average pack size low. Harvest and depredation removals also affect social and dispersal behavior (Adams et al. 2008, Brainerd et al. 2008, Ausband 2015). Additionally, pack turnover is now greater than in populations with less human-caused mortality.

Development of reliable methods to estimate territory size, territory overlap, and pack size is critical for accurate estimates of abundance. One means for developing models to estimate territories and pack sizes is an empirical modeling approach. This approach generally involves measuring and attempting to discern patterns in territory and pack size dynamics (e.g., Rich et al. 2012). Empirical models do not, however, provide an understanding of causal mechanisms, i.e., the underlying processes that shape the system and patterns we observe, such as processes driving decisions carnivores make about where to settle and whether to stay in or leave a social group. Ignoring causal mechanisms may yield models that do not suitably predict conditions beyond the spatiotemporal scale for which they were developed (Mitchell and Powell 2002). Empirical models may also require extensive continued monitoring and data collection to provide sufficient data for predictions.

An alternative method to empirical modeling is a mechanistic modeling approach. Such an

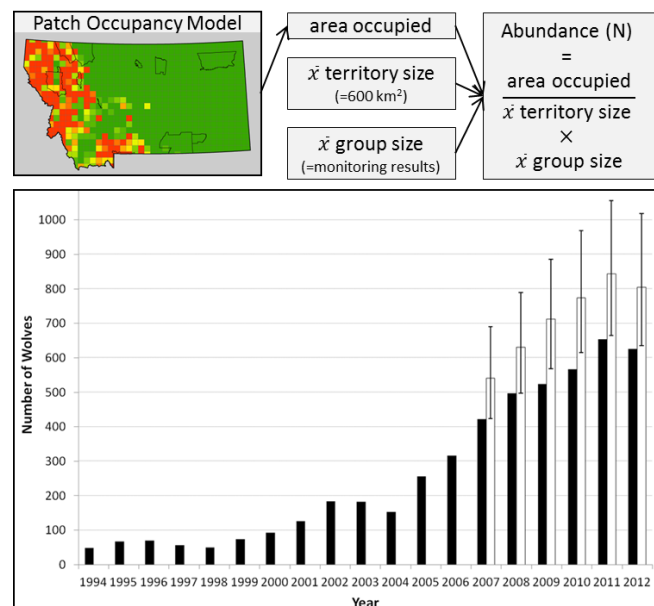


Fig. 7. Example of POM results (red indicates highest occupancy probability, green lowest), and methods for calculating abundance. Graphed abundance since 1994 is based on minimum counts (black bars) and POM-based estimates (white bars). (Adapted from Bradley et al. 2015.)

approach involves developing theoretical models that capture the hypothesized causal mechanisms structuring the system (Mitchell & Powell 2004, 2012). Predictions from these models can be compared to actual behaviors of animals to identify the model(s) with most support (Mitchell & Powell 2002, 2004, 2007, 2012). Resulting mechanistic models are based on the likely causal mechanisms that shape the system, and thus yield reliable scientific inference and are predictive at any spatiotemporal scale. Importantly, abundant data are not required for predictions.

2.2 Goals and General Approach

Our goal is to develop tools to estimate territory and group size of wolves to calibrate estimates of abundance of wolves in the Northern Rocky Mountains (NRM). To achieve this goal, our steps will be to:

1. **Develop a suite of mechanistic territory models.** These models will capture the potential causal mechanisms we hypothesize structure territories of wolves. We will run simulations to provide general predictions of territorial behavior under each model.
2. **Identify the most predictive territory model for wolves in Montana and Idaho.** We will parameterize the models from Step 1 with data for Montana and Idaho, and use the models to generate specific predictions of territorial behavior under each model. We will then compare these predictions to actual locations of GPS-collared wolves in Montana and Idaho. We will identify the best model as the one that most closely predicts real territorial behavior.
3. **Develop a suite of mechanistic group size models.** These models will capture the potential causal mechanisms we hypothesize structure social behavior of wolves. We will run simulations to provide general predictions of social behavior under each model.
4. **Identify the most predictive group size model for wolves in Montana and Idaho.** We will parameterize the models from Step 3 with data for Montana and Idaho, and use the models to generate specific predictions of social behavior under each model. We will compare these predictions to actual group sizes of wolves in Montana and Idaho as identified through monitoring data. We will identify the best model as the one that most closely predicts actual group sizes.
5. **Calibrate estimates of abundance.** We will use the best models for territory and group size alongside POM to calibrate estimates of abundance of wolves in the NRM.

2.3 Progress

Overview:

We are currently working on Step 1. There are 3 primary components under this step:

a) Develop a suite of mechanistic territory models.

We are designing the models based on theory of carnivore behavior. For example, theory states that carnivores are likely adapted to choose economic territories that maximize benefits of prey against costs such as travel, defense, competition, and predation (Darwin 1859, Brown 1964, Brown and Orians 1970, Emlen and Oring 1977, Krebs and Kacelnik 1991, Adams 2001). Like other carnivores, we also expect that wolves are adapted to defend the smallest territory possible that meets a threshold for survival and reproduction (Mitchell and Powell 2004, 2007, 2012). Each model will capture different ways we hypothesize wolves structure territories based on benefits and costs.

b) Run simulations of the models.

We are using the program NetLogo (Wilensky 1999) to conduct our simulations. In the simulations, the landscape is represented as a continuous grid of patches on which a pack forms a territory (e.g., Fig. 8). Each patch is associated with various benefits of prey, and the pack selects patches based on these benefits while considering costs associated with owning each patch as defined by the model (e.g., costs involving travel, defense, competition with neighboring packs, risk of predation by humans, etc.). The pack must also consider any constraints when forming the territory, such as rugged terrain. In each simulation, packs acquire patches for territories as economically as possible by trying to maximize benefits while minimizing costs. Each pack continues to build a territory until it acquires enough resources for survival and reproduction.

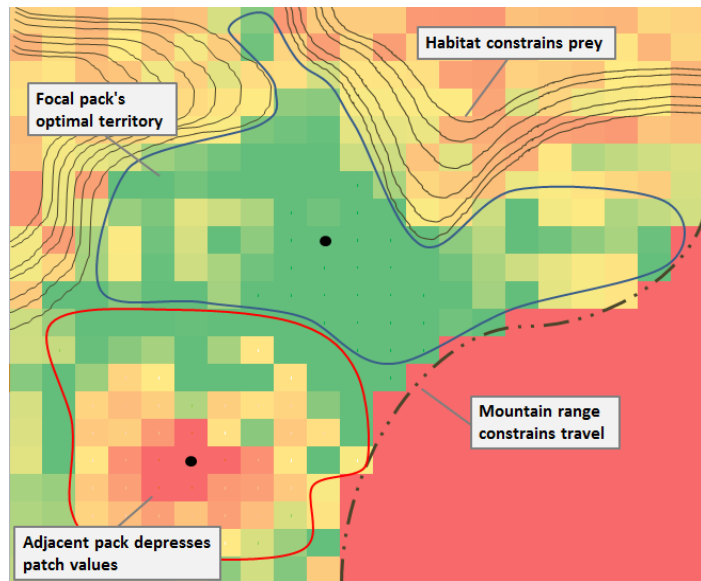


Fig. 8. Example of a simulated landscape. Colors indicate patch value (green = high, red = low), which account for benefits of prey and potential costs of ownership. Here, prey are constrained by topography to valley bottoms in winter. A mountain range negates values beyond it, and neighbors (red outline) depress patch value most heavily in the center of that territory. The blue outline represents the focal pack's optimal territory considering these benefits and costs.

c) Summarize results and make general predictions of territorial behavior that should be observed under each model.

We are developing general predictions of wolf territories under each model. If that model successfully captures wolf behavior then our predictions should be observed in real territories. We are using the program R (R Core Team 2014) to summarize results.

Example Model and Results—Territories Based on Benefits of Prey and Costs of Travel:

Model Explanation: Black bears (*Ursus americanus*) have been shown to structure their home ranges economically based on benefit of food resources and costs of travel (Mitchell and Powell 2012). Therefore, we constructed a model hypothesizing that wolves select territories based on benefits of prey and costs of travel (Fig. 9). We also wanted to evaluate how various prey distributions may affect territorial behavior in this model, so we simulated prey distribution as ranging from random to highly clumped in various landscapes (Fig. 10).

Analyses: We ran 1,200 simulations. In a single iteration, a pack forms a territory on one of these landscapes (e.g., Fig. 11). The pack stops forming its territory once it has met a threshold of resources needed for survival and reproduction (see Fig. 9). We fixed this threshold at 3 different settings to assess the effects of various thresholds. We ran 100 iterations for each of the 4 landscapes and 3 thresholds. We summarized results through various measurements, including A) total territory size (# of patches); B) travel patches (# of patches added as travel corridors to high-value patches); C) territory contiguity (proportion of the territory that was non-travel

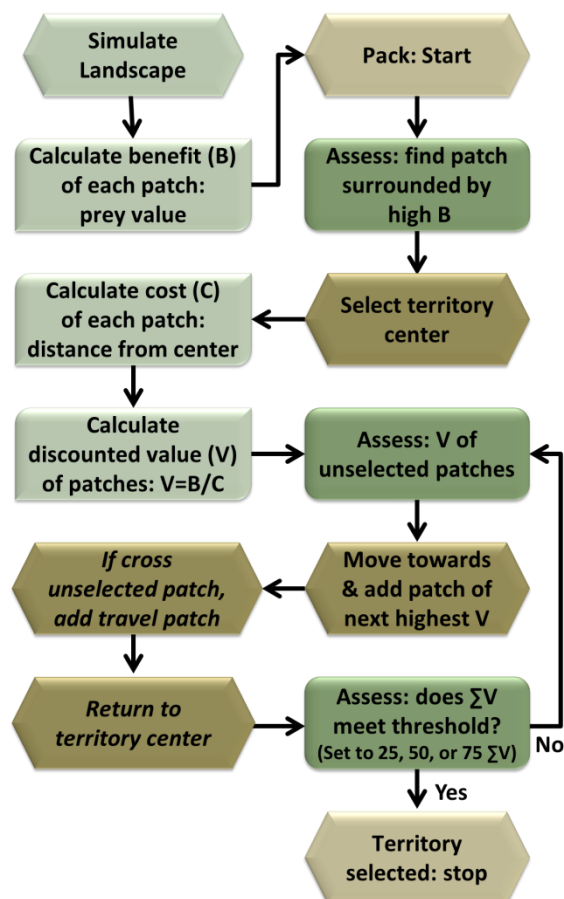


Fig. 9. Structure of territory simulations in the model based on prey and travel costs. A pack selects a territory economically by seeking patches that maximize benefits and minimize costs. It stops once it has met a simulated threshold for survival and reproduction.

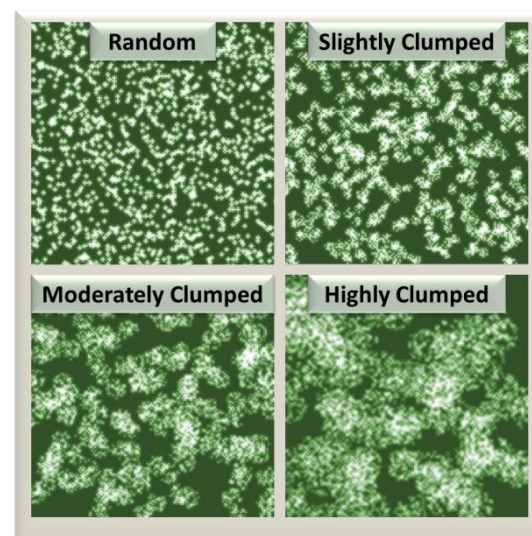


Fig. 10. Example simulated landscapes where prey distribution ranges from random to highly clumped. Lighter areas indicate patches of greater prey benefits. All landscapes have equal total benefits available and are 150x150 patches in size.

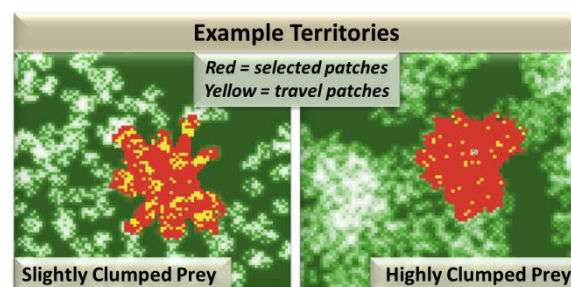


Fig. 11. Example results of 2 iterations showing how packs structured territories on 2 different landscapes.

patches); and D) territory efficiency (amount by which the mean benefits of prey within the territory exceeded the mean benefits of prey available on the landscape). We calculated these results by mean values for each landscape type and threshold level.

Preliminary results: Preliminary results suggest that if wolves structure territories based on benefit of prey and costs of travel, we would see several characteristics that vary according to prey distributions (Fig. 12). Prey distribution would affect territory size: as prey become more clumped, territory size decreases. Travel corridors within the territory also decrease as prey become more clumped, which leads to increased territory contiguity. Additionally, when prey are more clumped the efficiency of territories is higher, meaning that packs are able to select territories that better exceed the mean benefits available on the landscape.

From these results, we may expect territory size to differ regionally and seasonally. For example, wolf territories may be smaller in areas with clumped elk herds compared to areas with more dispersed deer populations. Territory size may also decrease and shift in winter when ungulates are more highly clumped. Seasonal change in territory size will be explored more thoroughly in subsequent models. Ungulate behavior and distribution will thus affect territorial behavior of wolves. Further analyses are ongoing.

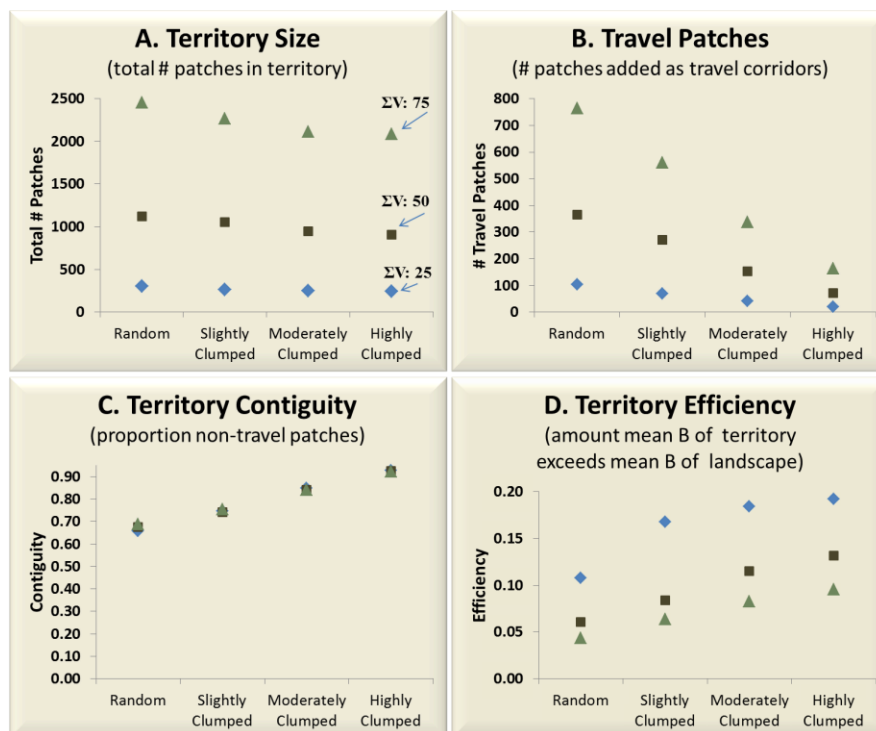


Fig. 12. Preliminary results from a model based on benefits of prey and costs of travel. We summarized results as A) total territory size (# of patches); B) travel patches (# of patches added as travel corridors to high-value patches); C) territory contiguity (proportion of the territory that was non-travel patches); and D) territory efficiency (amount by which the mean benefits of prey within the territory exceeded the mean benefits of prey available on the landscape). Results are summarized for each prey distribution (x-axis) and threshold level (i.e., total resources required for survival and reproduction, as indicated by symbols in A). Territory size decreases as prey distribution becomes more clumped, as do number of travel patches. This leads to increased contiguity. Efficiency is also greater when prey are more clumped. Effects are more pronounced at higher thresholds of resources.

Summary and Next Steps:

Our work to date provides a foundation from which we are building more complex models of territorial behavior. We are continuing to build the suite of territory models by adding levels of complexity and realism. For example, next we will investigate:

- How do other distributions, numbers, and behaviors of prey affect territories?
- How might costs of defense affect territorial behavior?
- How would costs of competition affect territorial behavior?
- How would risk of predation by humans (e.g., through harvest) affect territorial behavior?

Each model will provide general predictions of territorial behavior. In Step 2, we will parameterize the models with real data and generate specific predictions of territorial behavior for wolves in Montana and Idaho. We will then compare these predictions to territories of GPS-collared wolves to identify the most accurate model that predicts real wolf behavior. We will use similar approaches to develop group size models for Steps 3 & 4, as well. Alongside POM, in Step 5 these models will help accurately estimate abundance of wolves through biologically based, spatially explicit predictions for territory size, location, and overlap and group size.

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LITERATURE CITED

- Adams, L. G., R. O. Stephenson, B. W. Dale, R. T. Ahgook, and D. J. Demma. 2008. Population dynamics and harvest characteristics of wolves in the Central Brooks Range, Alaska. *Wildlife Monographs* 170:1–25.
- Ausband, D. E. 2015. Groups and mortality: their effects on cooperative behavior and population growth in a social carnivore. University of Montana.
- Ausband, D. E., C. R. Stansbury, J. L. Stenglein, J. L. Struthers, and L. P. Waits. 2015. Recruitment in a social carnivore before and after harvest. *Animal Conservation* 1–9.

- Ausband, D., M. S. Mitchell, K. Doherty, P. Zager, C. Mack, and J. Holyan. 2010. Surveying predicted rendezvous sites to monitor gray wolf populations. *Journal of Wildlife Management* 74:1043–1049.
- Besbeas, P., S. N. Freeman, B. J. T. Morgan, and E. A. Catchpole. 2002. Integrating mark-recapture-recovery and census data to estimate animal abundance and demographic parameters. *Biometrics* 58:540–547.
- Boertje, R. D., and R. O. Stephenson. 1992. Effects of ungulate availability on wolf reproductive potential in Alaska. *Canadian Journal of Zoology* 70:2441–2443. NRC Research Press Ottawa, Canada.
- Boitani, L., P. Ciucci, and A. Mortelliti. 2012. Designing carnivore surveys. Pages 8–30 *in* *Carnivore Ecology and Conservation A Handbook of Techniques*. Oxford University Press, Oxford, United Kingdom.
- Bradley, L., J. Gude, N. Lance, K. Laudon, A. Messer, A. Nelson, G. Pauley, M. Ross, T. Smucker, and J. Steuber. 2015. Montana gray wolf conservation and management 2014 annual report.
- Brainerd, S. M., H. Andren, E. E. Bangs, E. H. Bradley, J. A. Fontaine, W. Hall, Y. Iliopoulos, M. D. Jimenez, E. A. Jozwiak, O. Liberg, C. M. Mack, T. J. Meier, C. C. Niemeyer, H. C. Pedersen, H. Sand, R. N. Schultz, D. W. Smith, P. Wabakken, and A. P. Wydeven. 2008. The effects of breeder loss on wolves. *Journal of Wildlife Management* 72:89–98.
- Fuller, T. K., L. D. Mech, and J. Fitts-Cochran. 2003. Wolf population dynamics. Pages 161–191 *in* L. D. Mech and L. Boitani, editors. *Wolves: behavior, ecology and conservation*. University of Chicago Press, Chicago, Illinois.
- Goyal, S. M., L. D. Mech, R. A. Rademacher, M. A. Khan, and U. S. Seal. 1986. Antibodies against canine parvovirus in wolves of Minnesota: a serologic study from 1975 through 1985. *Journal of the American Veterinary Medical Association* 189:1092–4.
- Johnson, M. R., D. K. Boyd, and D. H. Pletscher. 1994. Serologic investigations of canine parvovirus and canine distemper in relation to wolf (*Canis lupus*) pup mortalities. *Journal of Wildlife Diseases* 30:270–273.
- Mech, L. D., L. G. Adams, T. J. Meier, J. W. Burch, and B. W. Dale. 1998. *The Wolves of Denali*. University of Minnesota Press, Minneapolis, Minnesota.
- Mech, L. D., and S. M. Goyal. 1995. Effects of canine parvovirus on gray wolves in Minnesota. *The Journal of Wildlife Management* 59:565.
- Miller, D. A. W., J. D. Nichols, J. A. Gude, L. N. Rich, K. M. Podrutzny, J. E. Hines, and M. S. Mitchell. 2013. Determining occurrence dynamics when false positives occur: estimating the range dynamics of wolves from public survey data. *PLoS ONE* 8:1–9.
- Mills, K. J., B. R. Patterson, and D. L. Murray. 2008. Direct estimation of early survival and movements in eastern wolf pups. *Journal of Wildlife Management* 72:949–954.
- Mitchell, M. S., D. E. Ausband, C. a. Sime, E. E. Bangs, J. a. Gude, M. D. Jimenez, C. M. Mack, T. J. Meier, M. S. Nadeau, and D. W. Smith. 2008. Estimation of successful breeding pairs for wolves in the Northern Rocky Mountains, USA. *Journal of Wildlife Management* 72:881–891.

- Mitchell, M. S., and R. A. Powell. 2002. Linking fitness landscapes with the behavior and distribution of animals. J. Bissonette and I. Storch, editors. *Landscape Ecology and Resource Management*. Island Press, Washington, D.C.
- Mitchell, M. S., and R. A. Powell. 2004. A mechanistic home range model for optimal use of spatially distributed resources. *Ecological Modelling* 177:209–232.
- Mitchell, M. S., and R. A. Powell. 2007. Optimal use of resources structures home ranges and spatial distribution of black bears. *Animal Behaviour* 74:219–230.
- Mitchell, M. S., and R. A. Powell. 2012. Foraging optimally for home ranges. *Journal of Mammalogy* 93:917–928.
- Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. *Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003)* 20–22.
- R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rich, L. N., M. S. Mitchell, J. A. Gude, and C. A. Sime. 2012. Anthropogenic mortality, intraspecific competition, and prey availability influence territory sizes of wolves in Montana. *Journal of Mammalogy* 93:722–731.
- Solomon, N. G., and J. A. French, editors. 1997. *Cooperative breeding in mammals*. Cambridge University Press.
- Sparkman, A. M., J. Adams, A. Beyer, T. D. Steury, L. Waits, and D. L. Murray. 2011. Helper effects on pup lifetime fitness in the cooperatively breeding red wolf (*Canis rufus*). *Proceedings of The Royal Society* 278:1381–1389.
- Stahler, D. R., D. R. MacNulty, R. K. Wayne, B. vonHoldt, and D. W. Smith. 2013. The adaptive value of morphological, behavioural and life-history traits in reproductive female wolves. *The Journal of Animal Ecology* 82:222–34.
- Su, Y.-S., and M. Yajima. 2015. R2jags: using R to run “JAGS.”
- U.S. Fish and Wildlife Service. 1994. The reintroduction of gray wolves to Yellowstone National Park and central Idaho. Final Environmental Impact Statement.
- Uboni, A., J. Vucetich, D. Stahler, and D. Smith. 2015. Interannual variability: a crucial component of space use at the territory level. *Ecology* 96:62–70.
- Wilensky, U. 1999. NetLogo. <http://ccl.northwestern.edu/netlogo/>. Center for Connected Learning and Computer-Based Modeling, Northwestern University, Evanston, IL.